

Climate Change Threatens a Fig-Frugivore Mutualism at its Drier, Western Range Margin

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Ficus rubiginosa (the Rusty Fig; Moraceae) provides a keystone food resource for a diverse array of vertebrate frugivores in eastern Australia. These frugivores, in turn, provide vital seed-dispersal services to the fig. The aims of this study were to investigate impacts of population size and climatic variation on avian-frugivore visitation to *F. rubiginosa* at the extreme western, drier margin of the species' range. Eighty-two bird species visited *F. rubiginosa* trees in this three-year study. Twenty-nine species were frugivores or omnivorous frugivore/insectivores. The number of ripe fruit in a tree had the greatest positive influence on frugivore visitation ($p < 0.0001$). Fig-population size influenced the assemblage of frugivore species visiting trees but not the number of frugivores or the rate of frugivore visitation. The number of ripe fruit in a tree was negatively associated with declines in rainfall, to total losses of standing crops through dieback and lack of crop initiation. Predicted long-term declines in rainfall across this region of eastern Australia and increased incidence of drought will lead to reduced crop sizes in *F. rubiginosa* and likely reduce the viability of local populations of this keystone fig. This will threaten the mutualism between *F. rubiginosa* and frugivores across the region.

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KEYWORDS: climate change, *Ficus*, fragmented habitat, range expansion, small populations

INTRODUCTION

Range shifts and/or local extinctions are increasingly becoming a reality for a wide diversity of organisms (Bergamini et al. 2009, Chen et al. 2009, Lenoir and Svenning 2013, McMenamin et al. 2008, Perry et al. 2005, Przeslawski et al. 2012, Thomas and Lennon 1999, Whitfield et al. 2007). Climate-change-induced temperature rises have been linked to many of these changes (Gottfried et al. 2012, Parmesan and Hanley 2015, Poloczanska et al. 2013). Modelling predicts that birds will come under increasing risk of catastrophic mortality events during heatwaves (McKechnie and Wolf 2010) and that increasing numbers of bird species will be at risk of at least local extinction in the future as a result of climate change. Habitat fragmentation and/or disturbance are also major causes of local avian-population declines or extinctions (Ford 2011a, Ford 2011b, Moran et al.

2009) and can have negative long-term effects on populations of both plants and their avian-frugivore seed-dispersers (Cordeiro and Howe 2001, Cordeiro and Howe 2003, Cosson et al. 1999, Tewksbury et al. 2002). The extent of any impact depends to some extent on the degree of mutual dependence between fruiting trees and avian visitors (Herrera 1984, Jordano 1987, Wheelwright and Orians 1982).

Frugivorous birds are well-known consumers of figs (Shanahan et al. 2001) and their dependency on *Ficus* fruit production at times when other plants are not in fruit is a major reason for the keystone status of fig trees (Lambert and Marshall 1991).

The mechanisms underlying climate-change and habitat-fragmentation effects on plants and their avian visitors, such as the longer-term consequences of habitat disturbance on fundamental ecosystem processes including seed dispersal, are still poorly understood. Frugivore visitation to *Ficus* species has been the subject of many surveys and studies

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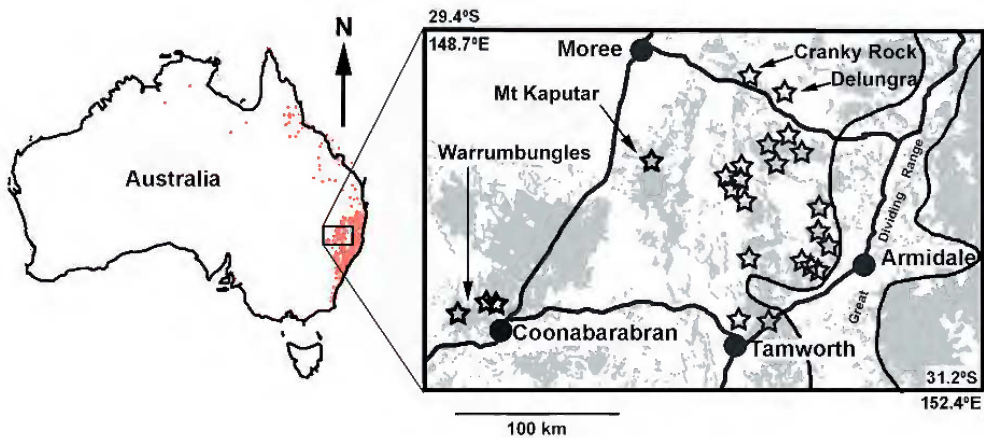


Figure 1. Distribution of *Ficus rubiginosa* in Australia (red dots; includes islands off the Queensland coast), and locations of the 24 study sites (stars) within the 50,000km² study area in northern New South Wales. Remaining areas of woody vegetation in the region are marked in grey on the map of the study area, based on satellite imagery (Google_Earth 2017).

(Bronstein and Hoffmann 1987, Goodman et al. 1997, Thornton et al. 2001, Lomáscolo et al. 2010, Schleuning et al. 2011). However, little attention has been given to the role fig trees play in supporting populations of avian frugivores in Australia beyond anecdotal observations. No studies of avian visitors to *Ficus rubiginosa* and/or their mutual dependence could be found in the literature. This is despite the keystone (Davic 2003, Paine 1969, Terborgh 1986) status of *Ficus* species, particularly the larger, monoecious species such as *F. rubiginosa* (Shanahan et al. 2001).

Ficus rubiginosa is the only large species of fig tree found commonly on the western, drier side of the Great Dividing Range in Queensland (Qld) and New South Wales (NSW). It is the most productive, fleshy-fruited tree in woodland and dry-rainforest habitats on the western side of the range, with a 2,500 km north-south distribution (Fig. 1). Many small populations of *F. rubiginosa* persist across the study area (Fig. 1), mostly in rocky habitats which are of little or no use for agriculture. Here, *F. rubiginosa* grows predominantly as a lithophyte and less frequently as a hemi-epiphyte (Dixon et al., 2001). It occurs as single isolated trees, in small populations in open, grazed landscapes or in small to large populations in dry-rainforest patches and open woodlands.

The primary aim of this study was to test a hypothesis concerning the provision of a keystone food resource by *F. rubiginosa* for frugivorous birds

at *F. rubiginosa*'s western, drier range margin. This hypothesis had three parts: (1) that *Ficus rubiginosa* provides keystone support to populations of avian frugivores at the western, drier edge of the species' range, (2) that climate change is leading to declines in fruit production by *F. rubiginosa* across this region, and (3) that the mutualism between *F. rubiginosa* and avian frugivores is under threat at the species' drier range margin on the western side of the Great Dividing Range in NSW.

MATERIALS AND METHODS

Study area and sites

This study was conducted in the New England Northwest region of New South Wales, between 29.4 and 31.2° south (200 km) and between 148.7 and 152.4° east (350 km) (Fig. 1).

The study area experiences warm to hot summers and cool to mild winters. Average annual rainfall varies from 600 mm to 800 mm west to east (BOM 2017). Altitudes across the study area range between 100 m and 1500 m with *Ficus rubiginosa* populations restricted to altitudes below 1000m (Atlas 2017). This region of eastern Australia has been extensively cleared for agriculture, with over 60% of the woody cover of natural vegetation having been cleared across the study area (Benson et al. 2010). This habitat clearing has left a patchwork of large and small remnants of

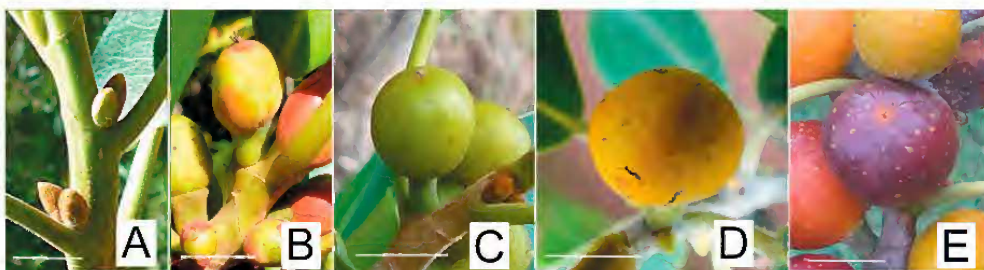


Figure 2. Five recognised stages of syconial development in the genus *Ficus*: A = bud stage, B = female-flowering stage, C = seed and fig-wasp development stage, D = male-flowering and wasp-emerging stage (pollinating fig wasps and non-pollinating fig wasps), E = ripe stage (Galil and Eisikowitch, 1968). Scale bars = 1 cm.

natural vegetation and single paddock-trees across the landscape. Twenty-four sites were established in the study area in 2014, evenly spread across three habitat-fragment/fig-population size-categories: category 1 = single trees growing within agricultural landscapes or disturbed vegetation (eight sites); category 2 = small populations of between five and fifteen fig trees growing within agricultural landscapes or disturbed vegetation (eight sites); category 3 = over fifty trees growing within contiguous natural vegetation (eight sites); (see Fig. 2 in Mackay et al. 2018 for Google Earth satellite images of examples of the three population sizes). The extreme western, drier range margin of *F. rubiginosa* extends in a north-easterly direction from the Warrumbungles National Park west of Coonabarabran through Mt Kaputar National Park and Cranky Rock near Delungra (Fig. 1). Additional

observations were conducted at five sites in mesic habitat within 50 km of the coast between October 2014 and September 2016. These five sites were between Coffs Harbour and Port Macquarie, over 150 km to the east of the inland study sites.

Fruit resources

The fruit of *Ficus rubiginosa*, as in other monoecious *Ficus* species, ripen more-or-less synchronously within crowns but asynchronously among crowns (Janzen 1979). Asynchrony in fruit development among trees results in ripening fruit being available across the breeding population of *F. rubiginosa* throughout the year except during harsh climatic conditions such as drought periods and cold winters (Mackay 2018). However, ripe fruit are not always available within sub-populations (e.g., within study sites), depending on climatic conditions and the number of trees in a site. Trees in which bird observations were recorded were categorised as either vegetative (non-fruiting) or according to recognised developmental stage/s of fruit in the trees ('stages A to E', Galil and Eisikowitch 1968; Fig. 2) and the number of fruit in trees. Ripening fruit turn yellow (stage D). Fruit ripen fully and turn red-brown (stage E) after the wasps have departed. Ripe and ripening fruit are usually on trees simultaneously (Fig. 3) except at early stages of ripening. Mention of the number of ripe fruit on trees in this paper, sometimes described as numbers of 'ripe-and-ripening fruit' on a tree for clarity,



Figure 3. D-stage (yellow, ripening) and E-stage (red, ripe) syconia. D- and E-stage syconia are 9 to 23 mm in diameter in *Ficus rubiginosa*. D and E syconia were almost always on branches simultaneously.

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refer to the total number of ripening D-stage and ripe E-stage syconia on trees together.

The total numbers of ripe-and-ripening fruit on trees were estimated by counting 1000 fruit and then extrapolating the area covered by that 1,000 fruit to the whole area of the tree when fruit production was observed to be even around the tree. In cases where fruit production was observed to be uneven over the tree (sometimes fruit production was higher on the northern, sunnier sides of trees) then second and/or further counts were made of 1000 fruit and extrapolated across areas of higher/lower fruit production. Fruit numbers were categorised into 5 logarithmic size-classes to minimise any inaccuracies in fruit-count estimates (categories: 1 = 0 to 20 fruit; 2 = 21 to 200 fruit; 3 = 201 to 2,000 fruit; 4 = 2,001 to 20,000 fruit; 5 = 20,001 to 200,000 fruit).

Avian visitors

Five hundred and sixty-two observation periods were conducted at these twenty-four sites over three years, from February 2014 to January 2017. Observations were spread across the three *Ficus*-population categories of single trees, small populations and large populations, and across the twelve months of the year. Observations were spread over all daylight hours. Each observation period was twenty-minutes in duration, considered to be a suitable or minimum survey period to capture bird species diversity and abundance at a tree (Fischer and Lindenmayer 2002a). Observations were conducted using binoculars (Barr and Stroud 'Sahara' 10x42 binoculars) from the cover of a hide and/or a nearby tree within ten to thirty metres of the observed trees. In each twenty-minute observation period all avian visitors to an individual, tagged tree were recorded. For each individual bird its identification, its activity (eating fruit, eating insects or insect products, or 'other' activities) and the length of time spent in the tree over the twenty-minute observation-period was recorded. Each bird was classified as a frugivore, insectivore or other based on individual birds' feeding activities during the observation periods. Species were then categorised based on individual birds' behaviour and categorisations were confirmed using the Birdlife Australia web site (birdlife.org 2017a) and the Handbook of Australian, New Zealand and Antarctic Birds (Higgins et al. 1990-2006). Frugivores also consumed insects (fig wasps) that were contained within ripe/ripening syconia. However, insect consumption was not recorded unless insects or insect products were directly consumed. Consumption of fruit was one aspect of seed dispersal observed in the study. However, not all frugivores

are necessarily good seed dispersers (Higgins et al. 1990-2006), and this was noted and mentioned for some species. Seed-dispersal behaviour of frugivores in and after leaving the fig trees was noted and compared/confirmed with published information in the literature about frugivores/seed dispersers. Dependent variables recorded in the 20-minute observation periods were the number of frugivore species, total number of frugivore individuals, and the total time spent in tree by frugivores (summed for all individual frugivores). Fourteen factors that potentially influenced frugivore visitation to fig trees were recorded: latitude, longitude, site, distance from observed tree to nearest non-isolated tree, fig-population size-category, number of trees in the population with ripe or ripening fruit, number of ripe and ripening fruit in the observed tree, date, month, season (3-month seasons of spring, summer, autumn, winter), time of day (Australian Eastern Standard Time), number of insectivore species, total number of insectivores, total time spent in tree by insectivores (summed for all individual insectivores). Fourteen twenty-minute observations were conducted in coastal populations of *F. rubiginosa* to confirm initial assessments made in the field and from the literature (Birdlife Australia 2018, Higgins et al. 1990-2006) that frugivores were present in greater diversity and abundance in mesic coastal regions than inland sites. These observations were compared with inland observations. All observations were conducted during fine, sunny weather.

A seed-germination experiment was conducted on regurgitated seed from the most common frugivore, the Pied Currawong, which was also the second-largest frugivore to visit *F. rubiginosa*. Forty regurgitated pellets, ten from each of four sites, were collected from the ground underneath feeding trees as well as distant from feeding trees and air-dried for later germination trials in glasshouse conditions. Pellets were broken up by hand immediately prior to planting in the glasshouse, and then spread over a soil-vermiculite mix (soil brought in from field sites where the pellets were collected) in plastic containers (standard, 17 x 12 x 3.5 cm take-away food containers, with holes drilled in the bottom for drainage) and placed under sprinklers to test if fig seeds in regurgitated pellets germinated with application of water alone.

Statistical analyses

Conditional Inference Tree analysis, using the Partykit package (Hothorn and Zeileis 2015) in R (R-Core-Team 2017), was used to assess which of the fourteen recorded input variables influenced

frugivore and insectivore visitation. Conditional Inference Trees, a recursive partitioning analysis, are especially useful for examining ecological data where input factors may interact hierarchically (De'Ath and Fabricius 2000, Jha and Vandermeer 2010). Conditional Inference Tree analysis is also unbiased, unlike other tree-structured regression models which have a selection bias towards categorical variables with more categories (Hothorn et al. 2006). Factors influencing frugivore visitation to fig trees were assessed at the 0.05 level of significance.

Linear mixed effects models (fixed and random effects) were constructed using methods outlined in Winter (2013) in R (R-Core-Team 2017) to analyse the data for frugivore visitation to trees. The Likelihood Ratio Test (Winter 2013) was used to attain p -values: saturated or 'full' models, using all measured factors ('effects'), were compared with alternative, 'reduced' models with each reduced model having a single factor removed, using the 'anova' function to determine Chi-square values, degrees of freedom, p -values and Akaike's Information Criterion (AIC) values (Burnham and Anderson 2003). The final fitted models accepted contained those factors which resulted in significant Chi-square values. Frugivore- and insectivore-visitation data were heteroscedastic and were log transformed for homoscedacity. Data for the dependent variable 'total time spent by frugivores in trees' were overdispersed so results from the LMER analyses were confirmed by constructing a General Linear Model in R (Lillis 2017, R-Core-Team 2017) with a quasipoisson model to deal with the overdispersion.

Analyses of variance (ANOVA) with multiple range tests were used to further examine the effect of fruit number on frugivore visitation.

A Chi-square test was used to test the null hypothesis of independence between frugivore visitation and bioregion (coast verses inland).

We conducted a follow-up survey of fruit production and frugivore visitation in the three *F. rubiginosa* populations in the Warrumbungles and a fourth site near Armidale in late September 2018 following a further twenty months of drought. This survey was conducted to test our predictions that fruit production by *F. rubiginosa* and frugivore visitation would both decline further if drought conditions persisted for longer periods than our three year study.

RESULTS

Hypothesis one was that *Ficus rubiginosa* provides support to populations of avian frugivores at the western, drier edge of the species' range.

Eighty-four bird species were recorded visiting *F. rubiginosa* over the three years of this study (Appendix 1). Twenty-nine of these species were frugivores, seven were both frugivore and insectivore and seven other species were neither frugivore nor insectivore, with the remainder being insectivores (Mackay et al. 2018). These trophic descriptions refer only to these birds' recorded behaviours in *F. rubiginosa* during the study. The majority of avian visitors recorded visiting *F. rubiginosa* in coastal populations were frugivores (107 frugivores from 10 species and 18 insectivores from 6 species, $n = 14$ twenty-minute observation periods). Fewer frugivores visited *F. rubiginosa* trees in drier, inland populations than in mesic, coastal populations ($F_{1,228} = 6.02, p = 0.015$), as well as fewer frugivore species ($F_{1,228} = 4.03, p = 0.046$) and less total time spent by frugivores in *F. rubiginosa* trees ($F_{1,228} = 8.90, p = 0.003; n = 562$ observation periods) per twenty-minute observation period. The majority of avian visitors recorded visiting *F. rubiginosa* in the drier inland region were insectivores (1686 insectivores from 54 species and 1051 frugivores from 27 species, $n = 562$ observation periods). Whilst there was lower diversity and abundance of frugivores observed in inland sites, *F. rubiginosa* trees remained an important food resource for a high diversity of frugivore species with 27 of the 29 frugivore species recorded in total being recorded in inland populations (Appendix 1). No difference was found in total frugivore numbers among *Ficus* population sizes. *Ficus rubiginosa* provided large numbers of fleshy fruit from early spring through autumn, when other fruit sources were often scarce or lacking within study sites and across the wider region.

Conditional Inference Tree analyses (see plots in Appendix 3) showed (1) that the number of frugivore species recorded in a tree was affected by the number of ripe fruit in the tree, the latitude (more frugivores in the two northern populations when the number of ripe fruit ≤ 20) and, in trees with between 200 and 2,000 ripening fruit, there was a negative relationship found between the number of frugivore species in a tree and the number of insectivores in the tree; (2) that the number of frugivores in a tree was most affected by the number of ripe and ripening fruit in the tree, with a steady increase in the number of frugivores as the number of fruit increased, with latitude affecting the number of frugivores in a tree to a minor degree with more frugivores visiting trees with fewer than 20 fruit at latitudes north of 29.923°S (i.e., the two northern populations in Fig. 1); and (3) that the time spent by frugivores in trees was significantly affected by only one of the input factors, the number of ripe fruit in the tree.

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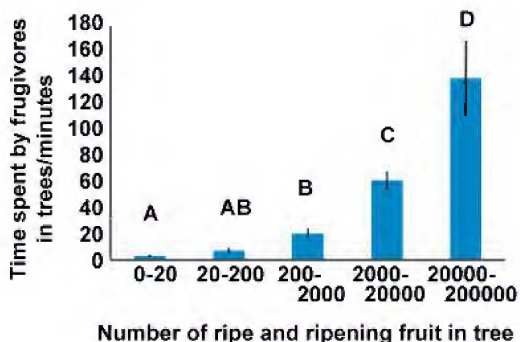


Figure 4. Mean total time (\pm SE) spent by frugivores in trees (minutes per twenty-minute observation period) against the number of ripe fruit in trees. Fruit numbers were categorised as shown on the x-axis. Letters (A, B, C, D) indicate significantly different means at $p < 0.05$ level).

Linear mixed effect (LME) analyses confirmed that the number of ripe-and-ripening fruit in a tree had a significant positive influence on the time spent by frugivores in trees ($\chi^2(1) = 178.79, p < 0.0001$); see Appendix 2. Further LME analysis showed that season influenced frugivore visitation, to a lesser extent than fruit number, with a peak in summer ($\chi^2(1) = 9.05, p = 0.0026$). Analysis of variance with a multiple range test further clarified the degree to which fruit number influenced the time spent by frugivores in trees (Fig. 4)

Seed germination experiment.

Each of the 40 Pied Currawong pellets collected and tested for fig-seed germination produced *Ficus rubiginosa* germinant seedlings. Between six and eighty-six *F. rubiginosa* seedlings germinated from each pellet.

Hypothesis two was that climate change is leading to declines in fruit production by *F. rubiginosa* in this region.

Initiation of A-stage syconia (buds, Fig. 2) was significantly reduced in response to lower rainfall (Mackay 2018). Pollination success, measured as percent of fruit set (i.e., as percent of A-stage syconia that developed to D stage) and as seed-to-flower ratios within fruit, declined significantly during periods of lower rainfall (by as much as 90%). Fruit production was further impacted by drought conditions which lead to partial to complete loss of crops to dieback (Fig. 5). Fire was observed to reduce fruit production in two ways: (1) by delaying fruit production in burnt



Figure 5. Loss of fruit and leaves through dieback of branch tips during drought conditions. Photographed in December 2014.

trees – trees remained vegetative for a period as they recovered (resprouted) after being burnt; (2) by reducing crop sizes in recovering trees – trees recovering from fire were always smaller than they had been before being burnt, at least for some time, and produced smaller crops than before being burnt (unpublished data).

Observations of fruiting by *F. rubiginosa* and visitation by frugivores in 2018 showed on-going decline in both measures as the drought continued and intensified. Of the 79 *F. rubiginosa* trees across the four populations, 77 were vegetative. Only two trees had crops of fruit, each with fewer than 200 very small, unripe fruit. No avian frugivores were recorded in the four sites in September 2018 except one Pied Currawong, an omnivore, in one of the Warrumbungles sites.

DISCUSSION

Hypothesis three was that the mutualism between *F. rubiginosa* and avian frugivores is under threat at the species' drier range margin on the western side of the Great Dividing Range in New South Wales.

This hypothesis is supported by the observations and experimental results from this research. The threat to this mutualism that we identified was declining rainfall. We showed that fruit production and frugivore visitation were significantly lower in response to lower rainfall, to drought and to fire. Crop sizes declined to zero in many trees and across many populations in response to drought conditions. This decline in fruit production had become almost

universally pervasive across all trees and populations at the three western-most sites by September 2018. Yet in the three years of this study from 2014 to 2017 September was in the middle of a peak in the production of ripe fruit from August to October, with a second, minor peak in January-February (Mackay 2018). This spring peak in fruit production and ripening coincided with the return of migratory and nomadic frugivores to the region. The observed decline is likely to continue into the future and possibly gather pace if climate-change predictions of lower rainfall, lower humidity, lower soil moisture and increased severity and frequency of droughts and fires (BOM 2018) are accurate. This would likely lead to a spiral of further decline and local extinctions in populations of *F. rubiginosa* and other, associated species including many of the frugivores we observed feeding in this tree. Consequences of such decline and local extinction would include community changes and ecosystem shifts on the western, drier side of the Great Dividing Range in NSW and Qld.

Similar patterns of decline have been predicted and reported in many woodland and forest habitats and to their avian species around the world (Brooks et al. 1999, Christiansen and Pitter, 1997, Hewson et al. 2007, Robinson and Wilcove 1994) including in Australia (Ford 2011a, Woinarski and Catterall 2004). Ford (2011a) lists extinction debt, habitat degradation, nest predation and declines in keystone food resources among the ecological processes contributing to the decline of woodland birds.

Many of the frugivores recorded feeding in *F. rubiginosa* trees in this study, particularly the larger species able to move longer distances among habitat fragments, are opportunists responding to available food resources. Hence large numbers of these birds congregate at fig trees when they are in fruit. Similarly large numbers of frugivores congregate at other plant species such as Native Olives, *Notolaea microcarpa*, when they are in fruit too. One reason for the keystone status of *F. rubiginosa*, though, is the fact it produces fruit at all times of the year and thus sustains populations of frugivores when other plant species are not in fruit. Channel-billed Cuckoos, specialist consumers of fruit and particularly figs (Moran et al. 2004, Birdlife-Australia 2017), were the second-most-frequent frugivore visitor to *Ficus rubiginosa* across the region with up to 14 of these large birds seen in fig trees at one time. Channel-billed Cuckoos (Fig. 6a) are migratory and were only recorded in the study region between September and February. Larger frugivores typically disperse seeds over longer distances than smaller birds (Ribeiro da Silva et al. 2015) and Channel-billed Cuckoos were the largest frugivore observed in this study. Owing

to their parasitic nesting behaviour, Channel-billed Cuckoos are not restricted to foraging near their nests but are able to forage more widely among fig populations on a day-to-day basis, often flying between populations of fig trees at night as well as during the day. On a seasonal basis, Channel-billed Cuckoos fly several thousand kilometres over the whole north-south range of *Ficus rubiginosa* and beyond (to northern Papua New Guinea) each year (Coates 1985). Channel-billed Cuckoos are thus likely to play an important role at the metapopulation scale as 'mobile links' among subpopulations (Lundberg and Moberg 2003), maintaining gene flow among them (Staddon et al. 2010) and facilitating range expansion in times of changing climates and habitats. More than half of all Channel-billed Cuckoos observed were in trees carrying more than twenty thousand ripe and ripening fruit. Channel-billed Cuckoos were not seen in areas that didn't contain fig trees with ripe fruit. Eastern Koels (Fig. 6b) are another frugivorous, parasitic-nesting cuckoo species commonly seen in *F. rubiginosa* (Appendix 1). They appeared to play a similar if lesser role in seed dispersal to Channel-billed Cuckoos. Fig Birds (Fig. 6c) are another migratory frugivore commonly seen feeding in fig trees including *F. rubiginosa*. Some species of avian frugivore recorded in this study were only recorded in coastal, mesic areas. These include the Wompoo Fruit Dove (Fig. 6d). Many pigeons, including the Wompoo Fruit Dove, are regarded as important seed dispersers (Wotton and Kelly 2012). Some other frequent visitors that consumed fruit were deemed to be potentially good seed dispersers based primarily on published literature (Birdlife Australia 2018, Higgins et al. 1990-2006), corroborated by personal observations. However, other frugivores recorded in this study were not considered good seed dispersers. These included Crimson Rosellas (Fig. 6e), which crushed the seed they consumed and usually consumed fruit when green, before seed was mature. Silvereyes (Fig. 6f) and other small frugivores were not considered good seed dispersers as they usually pecked at the fleshy walls of the fig fruit from the outside and left most seed behind.

Pied Currawongs were the most frequent frugivore species observed in this study (Appendix 1; up to 21 individual Pied Currawongs were observed in a tree at a time). Currawongs are large birds (44-51 cm, 285 g (oiseaux-birds.com)) and thus potentially efficient dispersers of *F. rubiginosa* seed (Ribeiro da Silva et al. 2015). Results from the germination trials and observations of currawong feeding behaviour reinforce this likelihood: feeding in fruiting *F. rubiginosa* trees often entailed filling their crops with fruit and then sitting quietly in a nearby tree

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Figure 6. Some of the avian frugivores recorded in *Ficus rubiginosa* during this study and referred to in the text: (a) Channel-billed Cuckoo (photo by KDM); (b) Eastern Koel (photo by KDM); (c) Wompoo Fruit Dove (photo by CLG); (d) Australian Figbird (photo by Camila Silveira de Souza); (e) Crimson Rosella (photo by KDM); (f) Silveryeye (photo by CLG).

whilst digesting the figs they had eaten, followed by regurgitation of indigestible plant material including fig seeds before returning to the feeding tree (personal observation). Pied Currawongs are also nest-predators known to prey on smaller woodland birds (Higgins et al. 1990-2006). This may counter their seed-dispersal service to *F. rubiginosa* if the birds they prey on are also seed dispersers. However, as mentioned above, larger birds such as Pied Currawongs are likely to be better seed dispersers than smaller species and the smaller bird species recorded in *F. rubiginosa* were mainly insectivores rather than frugivores (Mackay et al. 2018).

This study shows that *F. rubiginosa* provides a keystone (Paine 1969, Terborgh 1986, Davic 2003) food resource for a large and diverse array of avian-frugivore species. Total numbers of frugivores did not vary among *F. rubiginosa* population sizes. The species diversity observed in fig trees in the three different population-size categories (single trees, small and large populations) is likely a result of complex interactions between community composition, food resources, edge effects and distances to larger habitat patches (Laurance 2008a, Banks-Leite et al. 2011, Doerr et al. 2011). Such conjectures would need more work to elucidate precise links and causes between environmental factors and frugivore diversity but what this work shows conclusively is that fig trees in the Warrumbungles to Mt Kaputar region are providing an important food resource for avian frugivores and do so throughout the year, when other sources of fruit may be scarce.

Ecologists face enormous challenges in predicting the impacts of climate change on natural systems. However, this study shows that *F. rubiginosa* is a key component of remnant patches of dry rainforest that are scattered across our study area (Atlas 2017, Benson et al. 2010). The support provided by *F. rubiginosa* for frugivores in these habitats is likely to contribute to supporting and conserving entire natural communities in this region and beyond, including endangered semi-evergreen vine thickets, a class of dry rainforest. We conclude that the observed decline in fruit production and concomitant decline in frugivore populations are likely to lead to a compounding spiral of decline in other fleshy-fruited plant species in these dry rainforests. Furthermore, we are likely to see contractions and losses of dry-rainforest patches throughout the range of *F. rubiginosa* on the western side of the Great Dividing Range in NSW and Queensland if predictions of declining rainfall prove correct. This work highlights the need to study indirect impacts of climate change on species – via

process such as frugivory and seed dispersal for example. It also highlights the potential for different consequences of climate change such as longitudinal range shifts in response to rainfall changes as well as latitudinal shifts in response to temperature change.

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APPENDIX 1

Bird species	Family	Observed bird activity			Bird observations within fig population category:			Number observed in study sites
		eating fruit	eating insects	other	Single trees	5-15 trees	>50 trees	
Emu <i>Dromaius novaehollandiae</i>	Casuariidae	X				X		1
Common Bronzewing <i>Phaps chalcoptera</i>	Columbidae	X				X		5
Crested Pigeon <i>Ocyphaps lophotes</i>	Columbidae	X			X			4
Bar-shouldered Dove <i>Geopelia humeralis</i>	Columbidae	X				X		2
Wompoo Fruit Dove (coast only) <i>Ptilinopus magnificus</i>	Columbidae	X						0
Topknot Pigeon (coast only) <i>Lopholaimus antarcticus</i>	Columbidae	X						0
Eastern Koel <i>Eudynamis orientalis</i>	Cuculidae	X			X	X	X	25
Channel-billed Cuckoo <i>Scythrops novaehollandiae</i>	Cuculidae	X			X	X	X	106
Galah <i>Eolophus roseicapilla</i>	Cacatuidae	X			X			2
Crimson Rosella <i>Platycercus elegans</i>	Psittaculidae	X			X	X	X	91
Eastern Rosella <i>Platycercus eximius</i>	Psittaculidae	X			X	X	X	41
Rainbow Lorikeet <i>Trichoglossus moluccanus</i>	Psittaculidae	X			X	X	X	29
Satin Bowerbird <i>Ptilonorhynchus violaceus</i>	Ptilonorhynchidae	X				X		1
Spotted Bowerbird <i>Ptilonorhynchus maculatus</i>	Ptilonorhynchidae	X			X	X		12
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	Campephagidae	X			X	X	X	47
Australasian Figbird <i>Sphecotheres vieilloti</i>	Oriolidae	X			X	X	X	60
Pied Currawong <i>Strepera graculina</i>	Artamidae	X			X	X	X	265
Australian Magpie <i>Gymnorhina tibicen</i>	Artamidae	X			X	X		12
Little Raven <i>Corvus mellori</i>	Corvidae	X			X	X	X	26
Mistletoebird <i>Dicaeum hirundinaceum</i>	Dicaeidae	X				X	X	13
Common Starling <i>Sturnus vulgaris</i>	Sturnidae	X			X			15
Common Myna <i>Acridotheres tristis</i>	Sturnidae	X			X			4
Australian King-Parrot <i>Alisterus scapularis</i>	Psittaculidae	X	X			X		2

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Noisy Friarbird <i>Philemon corniculatus</i>	Meliphagi- dae	X	X		X	X	X	84
Spiny-cheeked Honeyeater <i>Acanthagenys rufogularis</i>	Meliphagi- dae	X	X		X	X	X	24
Red Wattlebird <i>Anthochaera carunculata</i>	Meliphagi- dae	X	X		X	X	X	93
Olive-backed Oriole <i>Oriolus sagittatus</i>	Oriolidae	X	X		X	X	X	33
Spangled Drongo <i>Dicrurus bracteatus</i>	Dicruridae	X	X			X		1
Silvereye <i>Zosterops lateralis</i>	Zosteropi- dae	X	X		X	X	X	183
Horsfield's Bronze-Cuckoo <i>Chalcites basalis</i>	Cuculidae		X		X			1
Shining Bronze-Cuckoo <i>Chalcites lucidus</i>	Cuculidae		X				X	2
Rainbow Bee-eater <i>Merops ornatus</i>	Meropidae		X		X			16
Red-winged Parrot <i>Aprosmictus erythropterus</i>	Psittacu- lidae		X			X		12
White-throated Treecreeper <i>Cormobates leucophaea</i>	Climacteri- dae		X		X	X	X	7
Red-browed Treecreeper <i>Climacteris erythroptus</i>	Climacteri- dae		X			X		4
Brown Treecreeper <i>Climacteris picumnus</i>	Climacteri- dae		X			X	X	6
Variegated Fairy-wren <i>Malurus lamberti</i>	Maluridae		X			X		1
Superb Fairy-wren <i>Malurus cyaneus</i>	Maluridae		X		X	X	X	333
Striped Honeyeater <i>Plectorhyncha lanceolata</i>	Meliphagi- dae		X			X		4
Little Friarbird <i>Philemon citreogularis</i>	Meliphagi- dae		X			X		2
Brown Honeyeater <i>Lichmera indistincta</i>	Meliphagi- dae		X			X		2
White-eared Honeyeater <i>Nesoptilotis leucotis</i>	Meliphagi- dae		X			X	X	17
Blue-faced Honeyeater <i>Entomyzon cyanotis</i>	Meliphagi- dae		X		X	X		14
Brown-headed Honeyeater <i>Melithreptus brevirostris</i>	Meliphagi- dae		X			X	X	16
White-naped Honeyeater <i>Melithreptus lunatus</i>	Meliphagi- dae		X				X	3
Eastern Spinebill <i>Acanthorhynchus tenuirostris</i>	Meliphagi- dae		X				X	2
Lewin's Honeyeater (coast only) <i>Meliphaga lewinii</i>	Meliphagi- dae		X				X	0
Singing Honeyeater <i>Gavicalis virescens</i>	Meliphagi- dae		X		X	X		68

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White-plumed Honeyeater <i>Ptilotula penicillata</i>	Meliphagi- dae		X		X	X	X	142
Yellow-faced Honeyeater <i>Caligavis chrysops</i>	Meliphagi- dae		X		X	X	X	69
Yellow-tufted Honeyeater <i>Lichenostomus melanops</i>	Meliphagi- dae		X			X		1
Noisy Miner <i>Manorina melanocephala</i>	Meliphagi- dae		X		X	X		125
Spotted Pardalote <i>Pardalotus punctatus</i>	Pardalotidae		X				X	6
Brown Gerygone <i>Gerygone mouki</i>	Acanthiz- idae		X			X	X	2
White-throated Gerygone <i>Gerygone olivacea</i>	Acanthiz- idae		X		X	X	X	9
Weebill <i>Smicrornis brevirostris</i>	Acanthiz- idae		X			X	X	23
White-browed Scrubwren <i>Sericornis frontalis</i>	Acanthiz- idae		X		X	X	X	67
Yellow-rumped Thornbill <i>Acanthiza chrysorrhoa</i>	Acanthiz- idae		X		X	X	X	108
Yellow Thornbill <i>Acanthiza nana</i>	Acanthiz- idae		X			X		3
Striated Thornbill <i>Acanthiza lineata</i>	Acanthi- zidae		X		X	X	X	183
Buff-rumped Thornbill <i>Acanthiza reguloides</i>	Acanthi- zidae		X		X	X	X	45
Brown Thornbill <i>Acanthiza pusilla</i>	Acanthi- zidae		X			X	X	88
Rufous Whistler <i>Pachycephala rufiventris</i>	Pachycep- halidae		X		X	X	X	5
Golden Whistler <i>Pachycephala pectoralis</i>	Pachycep- halidae		X				X	1
Grey Shrike-thrush <i>Colluricincla harmonica</i>	Pachycep- halidae		X		X	X	X	12
Dusky Woodswallow <i>Artamus cyanopterus</i>	Artamidae		X			X		2
Willie Wagtail <i>Rhipidura leucophrys</i>	Rhipidu- ridae		X		X	X	X	71
Grey Fantail <i>Rhipidura fuliginosa</i>	Rhipidu- ridae		X			X	X	36
Satin Flycatcher <i>Myiagra cyanoleuca</i>	Monarchi- dae		X			X		5
Restless Flycatcher <i>Myiagra inquieta</i>	Monarchi- dae		X		X		X	4
Apostlebird <i>Struthidea cinerea</i>	Corcora- cidae		X		X			14
Rose Robin <i>Petroica rosea</i>	Petroicidae		X		X		X	4
Scarlet Robin <i>Petroica multicolor</i>	Petroicidae		X		X			6

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Jacky Winter <i>Microeca fascinans</i>	Petroicidae		X			X	X	3
Eastern Yellow Robin <i>Eopsaltria australis</i>	Petroicidae		X			X		12
Fairy Martin <i>Petrochelidon ariel</i>	Hirundinidae		X			X		2
Welcome Swallow <i>Hirundo neoxena</i>	Hirundinidae		X		X	X		13
Laughing Kookaburra <i>Dacelo novaeguineae</i>	Alcedinidae			X		X		2
Yellow-tailed Black-Cockatoo <i>Zanda funereus</i>	Cacatuidae			X			X	1
Magpie-lark <i>Grallina cyanoleuca</i>	Monarchidae			X	X			14
Grey-crowned Babbler <i>Pomatostomus temporalis</i>	Pomatostomidae			X	X	X		24
Pied Butcherbird <i>Cracticus nigrogularis</i>	Artamidae			X	X	X	X	13
Red-browed Finch <i>Neochmia temporalis</i>	Estrildidae			X			X	4
Double-barred Finch <i>Taeniopygia bichenovii</i>	Estrildidae			X		X		15
TOTAL SPECIES		29	55	7	45	65	46	2821
Frugivore species					20	23	15	
Insectivore species					27	43	33	
Other species					4	6	3	

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APPENDIX 2

Number of frugivore species in trees ('Numfrugspp'):

A linear model of the number of frugivore species in a tree was fitted with the number of ripe fruit in a tree and the season as variables. This model was significant ($F_{2,559} = 203.5, p < 0.0001$). For each change of season from spring to summer there was, on average, a decline in the number of frugivore species of 0.12 ± 0.04 (SE) species. For each increase in the number of ripe fruits (categorized) there was an increase, on average, of 0.56 ± 0.03 (SE) frugivore species. The model fitted was: Number of frugivore species = $0.58 * \text{number of ripe fruit} - 0.12 * \text{season}$; the predicted number of frugivore species at the average number of ripe fruit = 0.75 ± 0.04 (estimated value \pm SE).

Number of frugivores in trees ('Numfrugs'):

As the random effects in the LMER analysis were not significant, the analysis was run again as a simple linear model with fixed effects only using the fixed effects that were significant in the LMER analysis. I constructed a linear model of the number of frugivores in a tree (numfrugs) as a function of the number of ripe fruit in the tree (numripefruit) plus the season (season) plus the number of insectivores in the tree (numinsecs) plus the number of insectivore species in the tree (numinsecsp). Thus, the null model was: numfrugs ~ numripefruit + season + numinsecs + numinsecsp. This model was significant ($F_{4,557} = 87.39, p < 0.0001$). However, collinearity problems required the removal of one or other of numinsecs and numinsecsp. Indeed, both variables had to be removed because of the non-linear relationship evident between insectivores and frugivores as fruit numbers increased above 20,000. Therefore the final linear model accepted was numfrugs is a function of the number of ripe fruit in a tree plus the season. This model was significant ($F_{2,559} = 167.1, p < 0.0001$). For each change of season from spring (1) to winter (4) there was a decrease, on average, of 0.31 ± 0.12 (estimated value \pm SE) frugivores. For each increase in the number of ripe fruit in a tree (categorized) there was an increase, on average, of 1.71 ± 0.10 (estimated value \pm SE) frugivores. The model fitted was: numfrugs = $1.71 * \text{numripefruit} - 0.31 * \text{season}$; predicted numfrugs at average numripefruit = 1.91 ± 0.13 (estimated value \pm SE).

Time spent by frugivores in trees ('Frugmins'):

Linear mixed effects model: Factors that impacted on time spent by frugivores in a tree (frugmins) were the number of ripe fruit (numripefruit) in the tree plus the season (season) plus the random factor 'site'. The number of ripe fruit affected the time spent by frugivores in a tree ($\chi^2(1) = 369.89, p < 0.0001$), increasing frugmins by $2.65 \text{ minutes} \pm 1.04$ (SE) for each increase in numripefruit. Season affected the time spent by frugivores in a tree ($\chi^2(1) = 7.28, p = 0.007$), decreasing frugmins by $0.87 \text{ minutes} \pm 1.05$ (SE) for each change in season from spring to winter.

Beginning with the best model from the LMER analysis I ran the following glm: glm(formula = frugmins ~ numripefruit + season + Site, family = quasipoisson()).

Numripefruit had the largest and most significant impact (estimate = 0.94689, $p < 0.0001$). Season was found to be **not** significant in this GLM. Site is still significant but has only a slight impact (estimate = 0.008964, $p = 0.0221$).

A one-way ANOVA conducted on $\ln(1+x)$ -transformed data produced a highly significant result: $F_{4,557} = 131.13, p < 0.0001$ (Kruskall-Wallis test statistic = 264.45, $p < 0.0001$) (Fig. 4.12). The impact on the time spent by frugivores in trees from an increase in the number of ripe fruit in the tree was approximately 1.7 minutes per fruit category (95% CI = 1.4 to 2.0 minutes, averaged over the 5 categories).

A GLM fitted to time spent by frugivores in a tree with season as the only variable was highly significant ($p < 0.001$). The impact of season on in a tree is approximately 0.3 minutes reduction each season from spring to winter.

APPENDIX 3

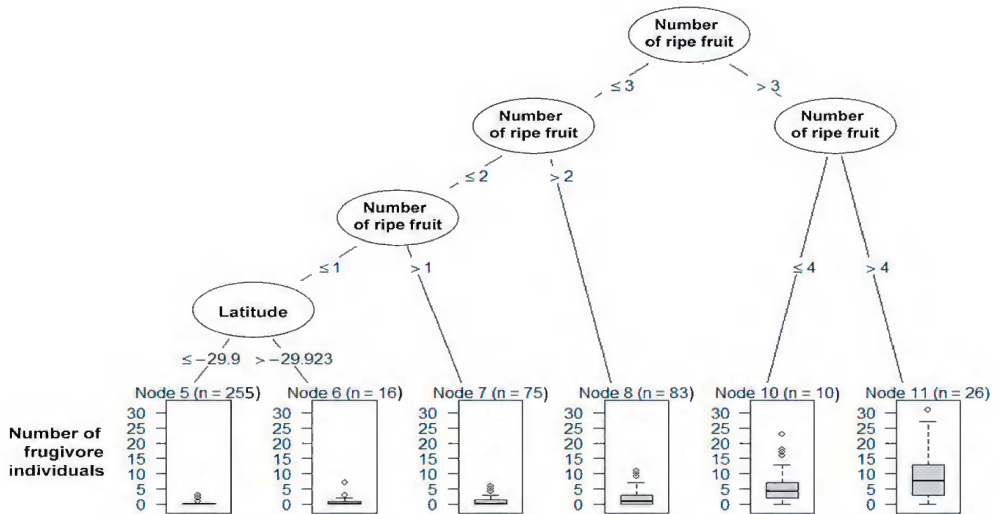


Figure A3.1. Results of Conditional Inference Tree analysis of number of frugivores per 20-minute observation period. The only significant factors were the number of ripe fruit in the tree (with splits at 20 fruit, 200 fruit, 2,000 fruit and 20,000 fruit) and, when there was zero to 20 fruit in a tree, latitude (with a split at 29.9°S i.e., more frugivores in the two northern populations)

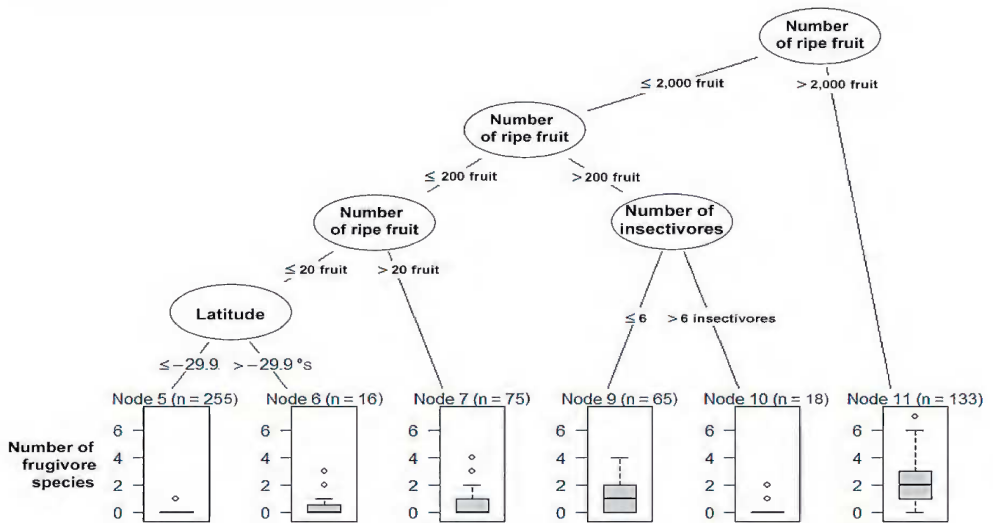


Figure A3.2. Results of Conditional Inference Tree analysis of mean number of frugivore species /minutes per 20-minute observation period. Significant factors were the number of ripe fruit in the tree (with splits at 20 fruit, 200 fruit, and 2,000 fruit) and, when there was zero to 20 fruit in a tree, latitude (with a split at 29.9°S, i.e., below the two northern populations; see map Fig. 4.1) and, when there were 200 to 2,000 fruit in a tree (category 3), the number of insectivores in the tree (fewer frugivores when there were more than 6 insectivores).